COMPARATIVE ECOLOGY OF BOBWHITE AND SCALED QUAIL IN MESQUITE GRASSLAND HABITATS

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COMPARATIVE ECOLOGY OF BOBWHITE AND

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GRASSLAND HABITATS

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PREFACE

This study was conducted to provide information on several aspects of the ecology of sympatric bobwhite and scaled quail in southwest Oklahoma. The information provided herein should enable biologists to better understand the effects of interspecific competition between these 2 game species.

Funds for this project were provided in part by the Oklahoma State University Resources Institute in conjunction with the Oklahoma Cooperative Wildlife Research Unit.

The 3 chapters of this thesis were prepared according to the formats of 3 scientific journals. Each chapter is complete in itself and requires no supportive material. Chapter I is in the format of the *Journal of Wildlife Management*. Chapter II follows the format of the *Journal of Wildlife Diseases* and Chapter III follows the format of *The Southwestern Naturalist*.

I express appreciation to my major adviser, Dr. John S. Barclay, for his assistance during the proposal and planning stages of this project, and for his advice and comments throughout the duration of the study. I am grateful to Dr. John A. Bissonette, Dr. Stanley F. Fox, Dr. Thomas A. Gavin, and Dr. James H. Shaw for serving on my graduate committee and providing advice and comments during the preparation of this thesis. Dr. William D. Warde provided assistance with much of the statistics herein. David H. Gordon provided able editorial assistance during the preparation of this thesis.

A hearty thanks is due to all the hunters who donated quail during this study, but especially to Gene Stout, Fish and Wildlife Manager, Fort Sill Military Reservation, Mike Cary, Keven Defoor, Tim McGee, and Warren Nell for their generous assistance.

A very special thanks is extended to my parents, Ernest and Joye Rollins, for their many years of support, both moral and financial, during all the years of my education. This thesis is dedicated to them.

Finally, I wish to thank my wife, Kay, for patience, understanding, and belief in me during the preparation of this thesis.

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CHAPTER I

FOOD HABITS OF SYMPATRIC BOBWHITE AND SCALED QUAIL IN OKLAHOMA[1]

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Abstract: Fall-winter food habits of sympatric bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) in southwestern Oklahoma during 1978-80 were compared using analysis of crop contents. A high degree of overlap was present between the 2 species for 1978-79 (Overlap coefficient C=0.65) and 1979-80 (C=0.88). Staple items included seeds of wheat, mesquite (*Prosopis glandulosa*), broomweed (*Gutierrezia dracunculoides*), and several others. Frequency of occurrence of broomweed seeds increased as the winter progressed in 1979-80, possibly because of low availability of more preferred foods. Interspecific competition for food resources may become important during late-winter months when seed supplies are decreased. Implications of competitive exclusion are discussed.

Bobwhite and scaled quail are sympatric over a large part of

[1] Supported in part by Oklahoma State University and the Oklahoma Cooperative Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, U.S. Fish and Wildlife Service, Oklahoma State University, and Wildlife Management Institute, cooperating).

Texas, and portions of Oklahoma, Colorado, and New Mexico. Both species are granivorous, shrub-grassland birds having similar diets but different habitat preferences (Schemnitz 1964). Bobwhites prefer a more "closed" habitat, with substantial grass cover (Hamilton 1962, Schemnitz 1964, Tharp 1971, Brown 1978), while scaled quail prefer a more "open" habitat with less grass cover (Wallmo 1956, Schemnitz 1964, Tharp 1971, Goodwin and Hungerford 1977).

The sympatric occurrence of these 2 important game species provides an opportunity to evaluate the degree of overlap in their diets. Several food studies have been conducted for scaled quail, but only in areas where bobwhites were absent (Wallmo 1956, Barkley 1972, Campbell et al. 1973, Davis and Banks 1973, Davis et al. 1975) or present only in relatively low numbers (Schemnitz 1961). Jackson (1969) conducted food studies for bobwhites where densities of the 2 species were more comparable, but did not report scaled quail food habits.

Schemnitz (1964) compared the diets of sympatric bobwhite and scaled quail in the Oklahoma panhandle and found that foods comprising 95% by volume of bobwhite diets comprised 73% of scaled quail diets. This high degree of similarity was present despite the distinct separation in preferred habitats of the 2 species. Bobwhites were found predominantly in bottomlands while scaled quail were found more often in more xeric uplands. In this study, I compared food habits in a more homogeneous habitat where habitat preferences were not as marked and home ranges more likely to overlap.

I thank M. Cary, T. McGee, and G. Stout for their assistance with collection of quail; J. Bissonette, S. Fox, T. Gavin, and D. Gordon for their comments and critical review of this manuscript; and J. S. Barclay

for his counsel and support throughout the study.

STUDY AREA

The majority of the sympatric range was characterized by a mesquite-grassland usually referred to as the Rolling Plains (Jackson 1969). The study area of approximately 80 km^2 was located in extreme southwestern Oklahoma in southern Harmon County. Primary land uses of the area were cattle grazing, interspersed with dryland wheat and cotton farming. The majority of the native pastures were infested to varying degrees with mesquite; lotebush (*Condalia obtusifolia*) and netleaf hackberry (*Celtis reticulatus*) were less common. Overgrazing was widespread, as indicated by the abundance of broomweed (*Gutierrezia dracunculoides*) and pricklypear (*Opuntia* sp.). Dominant grasses included blue grama (*Bouteloua gracilis*), side-oats grama (*B. courtipendula*), dropseeds (*Sporobolus* spp.), and buffalograss (*Buchloe dactyloides*). A detailed floral description was provided by Barber (1979). Gypsum outcrops and narrow, untillable ravines were common throughout the area. Topography, climate, and soils for this area were described by Barber (1979) and Morrison and Lewis (1976).

METHODS

Quail were collected by shooting during the regular 1978-79 and 1979-80 (20 November - 1 February) hunting seasons, utilizing hunter donations whenever available. Additional birds were collected in February and October 1979. Bobwhite and scaled quail were collected within 1 km of one another. Seven quail (4 bobwhites, 3 scaled quail) were collected from mixed coveys.

Birds were frozen, transported to the laboratory, and crops removed. Crop contents were oven dried, segregated to species, and measured volumetrically using water displacement to the nearest 0.1 cm^3. Foods present in less than 0.1 cm^3 were recorded as trace items. Seed identification was facilitated by the seed collection of the Oklahoma Cooperative Wildlife Research Unit and by Martin and Barkley (1961). Frequency of occurrence and percent total volume (Martin et al. 1946) were recorded for each food item. Plant names follow the nomenclature of Waterfall (1972).

The degree of overlap in diet (C_o) was computed using a modified version of the formula reported by Horn (1966). The formula is:

$$C_o = \frac{2 \sum_{i=1}^{t} B_i S_i}{\Sigma B_i^2 + \Sigma S_i^2},$$

where t is the total number of food species and B_i and S_i are the proportions of the total diet of bobwhite (B) and scaled (S) quail taken from food species i. A coefficient of 0.0 indicates no overlap while a value of 1.0 indicates complete overlap.

RESULTS AND DISCUSSION

Diets of sympatric bobwhite and scaled quail exhibited a high degree of overlap in both 1978-79 (C_o=0.65) and 1979-80 (C_o=0.88). The major foods of both species were primarily agricultural grains and seeds of forbs, with insects and green vegetation consumed in lesser amounts (Table 1). Foods that comprised 94.2% of the scaled quail's diet constituted 96.1% of the bobwhite's diet. Schemnitz (1961, 1964) found

Table 1. Crop contents of sympatric bobwhite and scaled quail collected November 1978 - February 1979 and October 1979 - January 1980 from Harmon County, Oklahoma.

	Bobwhite				Scaled Quail			
	1978-79 (*n*=16)		1979-80 (*n*=48)		1978-79 (*n*=49)		1979-80 (*n*=86)	
Foods	Freq.[a]	Vol.[b]	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.
Seeds								
Wheat	12	16.3	58	56.0	18	13.9	43	34.5
Broomweed (*Gutierrezia dracunculoides*)	0	0.0	50	11.6	4	t[c]	65	14.3
Western ragweed (*Ambrosia psilostachya*)	12	7.4	40	3.9	0	0.0	28	7.4
Buffalobur (*Solanum rostratum*)	49	9.6	6	t	55	5.4	27	6.3
Flax (*Linum* sp.)	19	1.1	29	4.9	29	0.2	47	6.4
Mesquite (*Prosopis glandulosa*)	25	3.5	12	1.3	57	13.9	16	1.0
Spurge (*Euphorbia* spp.)	62	10.3	15	0.7	26	10.4	7	0.2

Table 1. (Continued)

Foods	Bobwhite				Scaled Quail			
	1978-79		1979-80		1978-79		1979-80	
	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.
Sorghum (*Sorghum bicolor* and *S. bicolor* X *S. sudanense*)	12	11.7	15	5.9	0	0.0	19	8.1
Johnsongrass (*S. halepense*)	19	1.4	27	6.5	2	0.1	9	0.4
Doveweed (*Croton texensis*)	25	5.3	8	0.4	20	1.5	7	0.1
Sunflower (*Helianthus* sp.)	0	0.0	8	0.8	0	0.0	9	0.7
Loco (*Astragalus* spp.)	0	0.0	2	0.4	0	0.0	29	3.9
Russian thistle (*Salsola kali*)	25	3.2	0	0.0	31	5.8	14	1.8
Smartweed (*Polygonum* sp.)	6	1.8	4	0.8	6	t	15	1.2
Netleaf hackberry (*Celtis reticulatus*)	12	1.1	0	0.0	18	9.1	5	0.4
Thistle (*Cirsium texanum*)	0	0.0	23	1.1	10	0.1	19	0.9
Grama grasses (*Bouteloua* spp.)	19	0.7	21	1.5	10	0.5	20	0.8
Pigweed (*Amaranthus* spp.)	12	4.2	12	0.1	61	2.9	23	0.6

Table 1. (Continued)

	Bobwhite				Scaled Quail			
	1978-79		1979-80		1978-79		1979-80	
Foods	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.
Foxtail (*Setaria* sp.)	36	2.1	4	t	26	3.9	0	0.0
Erect dayflower (*Commelina crispa*)	12	8.5	0	0.0	2	t	0	0.0
TOTAL SEEDS IN COMMON		90.7		95.9		70.1		89.6
Green vegetation	69	4.6	48	1.9	59	16.1	59	8.8
Insects	56	1.1	21	1.9	31	2.1	12	1.0
TOTAL FOODS IN COMMON		96.4		99.7		88.3		99.4
Miscellaneous foods		3.6		0.4		11.6		0.6
TOTAL FOODS		100.0		100.1		99.9		100.0

[a]Frequency of occurrence expressed as percent of total crops

Table 1. (Continued)

[b]Percentage of total volume

[c]Items present in less than 0.1% of the total volume

that 95.2% of the bobwhite's diet constituted 73.5% of the scaled quail's diet (C_o=0.87) despite marked habitat preferences of the 2 species in the Oklahoma panhandle.

Both bobwhite and scaled quail have been shown to actively select preferred food items (Davis et al. 1975), therefore a plant may be highly utilized and yet be uncommon or low in abundance. Plant and seed availability data were not collected to determine if foods selected were eaten because preferred or due to great availability, or both. Differences in diet and food preferences may be detected however, since items available to bobwhites appeared to be equally available to scaled quail.

Although 38 different plant species were represented, only a few staple items comprised the majority of the diets. Schemnitz (1969, 1964), Campbell et al. (1973), and Davis et al. (1975) also considered relatively few items to be staples despite a wide range of foods utilized.

The main dissimilarity in diets found in this study was the number of different food species per crop. Scaled quail had a mean of 6.1 food species per crop, significantly (t=1.8, P<0.05) higher than the average of 4.9 items per crop for bobwhites. Schemnitz (1961, 1964) also found that scaled quail consumed a greater variety of foods ($\overline{X}$=8.1) than did bobwhites ($\overline{X}$=6.3).

The study area was, for the most part, severely overgrazed. Although grazing may be detrimental to residual grass cover important for roosting and nesting cover (Brown 1978), it did not appear to limit seed production of the area. Of the native food items common to both species, only flax (*Linum* sp.) is not considered an increaser or invader

(Rommann et al. 1979). Schemnitz (1961) also reported that grazing did not decrease seed availability to scaled quail in the panhandle of Oklahoma.

Wheat was the most important food (in terms of percent total volume) for bobwhites in both years, and for scaled quail in 1979-80. Wheat ranked second to green vegetation for scaled quail in 1978-79. These findings contrast with Schemnitz's (1961, 1964) results, where he found wheat of minor importance in fall-winter diets of bobwhite and scaled quail, despite its widespread availability. Wheatfields often interface with native mesquite pastures in Harmon County, allowing quail to feed in open fields without being far from escape cover. In all instances (N=8, 2 bobwhite, 6 scaled quail) that quail were observed actively feeding in wheatfields, coveys were within 15 m of available escape cover.

The majority of the wheat available appeared to be a result of waste from the previous year's harvest and "volunteer" growth. However, at least some newly sown seeds were eaten as indicated by the presence of seeds covered with a pink, antifungal chemical, Ceresan (methylmercury 2,3-dihydroxypropyl mercaptide and methylmercury acetate) which is placed on wheat seeds prior to sowing. No records of treated seed ingestion were made for the 1978-79 field season, but in 1979-80, 3 of 48 (6.2%) bobwhite crops and 4 of 82 (4.9%) scaled quail crops examined contained at least 1 treated seed. One bobwhite and 1 scaled quail had each consumed 2 treated seeds. Tucker and Crabtree (1970) suggested that Ceresan may be lethal to bobwhites. The possible impact of this chemical should be evaluated in order to determine its effect on wild quail.

The increased utilization of wheat by both species in 1979-80 may have been a result of its prolonged availability. Wheat normally sown in September germinates soon thereafter and presumably becomes unavailable for quail. Because of low soil moisture, the bulk of wheat planted in September and October 1979 did not germinate. Poor stands of wheat predominated throughout the 1979 field season. Reduced germination and hence greater availability, would have allowed both species of quail to utilize wheat to a greater degree than might be expected in more "normal" years.

There was considerable annual variation in the diets. Mesquite was a staple food item for both species in 1978-79, but comprised less than 2% of the diet of either species in 1979-80. This change may have been due, in part, to reduced seed availability. Several inches of rain fell on the study area during July 1979, approximately the same time mesquite was flowering. Rainfall knocking the flowers off the plants may have been responsible for the poor "bean" crop observed. Other studies (Jackson 1969, Campbell et al. 1973, Davis et al. 1975) indicated mesquite seeds were a major constituent and a preferred item in the diets of bobwhite (Texas) and scaled quail (New Mexico).

The apparent decrease in availability of some of the more staple foods was reflected by the high occurrence of broomweed in diets during 1979-80. Broomweed was found only in trace amounts in scaled quail and was absent in bobwhites in 1978-79. However, broomweed seeds were found in over 50% of the crops examined and comprised at least 10% by volume of the diet of both species in 1979-80. Davis and Banks (1973) concluded that Gutierrezia was a non-preferred item. Presumably, as larger and more preferred seeds became scarce, quail consumed more of the less preferred, but highly plentiful broomweed seeds. Jackson (1969:48) stated that broomweed may have been largely responsible for quail survival during harsh winters in the Texas panhandle. In addition to being an important food source, broomweed is excellent screening cover (Jackson 1962) allowing bobwhites to forage with more security.

The monthly occurrence of broomweed and other food items found in quail crops is presented in Table 2. As the occurrence of such items as wheat, western ragweed (Ambrosia psilostachya), and insects declined, the utilization of broomweed, green vegetation, and Russian thistle (Salsola kali) increased. Green vegetation (Baumgartner et al. 1952) and Russian thistle (Jackson 1969:48) tend to increase in occurrence when more preferred items are scarce. Occurrence of Russian thistle in scaled quail crops increased as the winter progressed, but was not found at all in bobwhites in 1979-80.

Green vegetation was a staple item for both species during both years of the study. Scaled quail consumed about 4 times more green vegetation by volume than did bobwhites. Schemnitz (1961, 1964) also found that scaled quail consumed more green material than did bobwhites (2.8% and 0.9%, respectively). Campbell et al. (1973) and Davis et al. (1975) found that green vegetation comprised 8-10% of the fall-winter diet of scaled quail in New Mexico.

Spikelets of grama grasses (Bouteloua spp.), despite their apparent availability, consistently amounted to less than 2% of the diet of either species. Low use of grama grasses has also been reported by Schemnitz (1961), Jackson (1969), Campbell et al. (1973), and Davis et al. (1975).

Insects (primarily Orthoptera and Coleoptera) were found in quail crops in amounts ranging from 1-2% each year. Previous studies in New

Table 2. Monthly occurrence of selected foods found in sympatric bobwhite and scaled quail collected October 1979 - January 1980 from Harmon County, Oklahoma. Numbers represent frequency of occurrence as expressed in percent of total crops examined.

	October		November		December		January	
	Bobwhite	Scaled	Bobwhite	Scaled	Bobwhite	Scaled	Bobwhite	Scaled
Common name	(6)[a]	(7)	(16)	(42)	(21)	(27)	(5)	(10)
Broomweed	0	0	56	64	71	81	0	70
Wheat	67	58	81	60	43	22	40	20
Ragweed	67	43	50	41	33	7	0	20
Green vegetation	50	20	44	52	52	70	40	80
Insects	67	14	25	17	9	7	0	0
Russian thistle	0	0	0	0	0	30	0	40

[a] Sample size

Mexico (Davis and Banks 1973, Campbell et al. 1973, Davis et al. 1975) and the Oklahoma panhandle (Schemnitz 1961, 1964) reported that insects comprised 5-8% of fall-winter diets. Decreased utilization of insects in the current study may be related to decreased abundance. The winters of 1977-78 and 1978-79 were more severe than normal (U. S. Department of Commerce 1978, 1979) and may have depressed insect populations.

Potential of Interspecific Competition for Foods

Whenever 2 closely related species having similar niches occupy the same range, the potential for interspecific competition exists. The amount of resource competition should be proportional to the degree of overlap if the resource is scarce (Pianka 1975:193). My data indicate that, within the same habitats, bobwhite and scaled quail consume essentially the same diets. A. S. Jackson (pers. comm.) suggested that diets of bobwhite and scaled quail are dictated by abundance of specific food items, and if availability is equal for both bobwhites and scaled quail, diets of both species should be very similar.

Before competition for a resource can occur, the resource must be in short supply (Cody 1974:203). Although wheat is heavily utilized by both species, most likely it is sufficiently available to preclude competition, at least until weather conditions favor germination and the subsequent loss of available seeds. As winter progresses, availability of seeds decreases and the degree of food competition may increase.

Seed availability may be affected by other species, including rodents (Jackson 1962) and other granivorous birds (Parmalee 1953). Harmon County harbors numerous migrant mourning doves (*Zenaida macroura*) (Morrison and Lewis 1976). In a study located approximately 20 km southeast of the current study, Morrison and Lewis found that wheat, haygrazer (Sorghum bicolor X S. sudanense), spurge (Euphorbia sp.), pigweed (Amaranthus spp.), and other species were important as early winter dove foods. Most of the wintering doves arrived in November and remained until March, or throughout the entire period of low seed availability. Doves were not collected during this study, but the data of Morrison and Lewis (1976) suggest that food competition analyses between quail may be confounded by seed depletion as a result of wintering doves. Parmalee (1953) concluded that large flocks of migrant mourning doves could be serious competitors with bobwhites for seeds in north-central Texas. Conversely, Griffing and Davis (1976) concluded there was little overlap between scaled quail and dove food habits in southeast New Mexico. This apparent contrast between Parmalee's and Griffing and Davis's findings may be a result of habitat differences between their study sites, different densities of doves, or some other factors.

Competitive Exclusion Principle

Quail production and food availability in the Rolling Plains are largely determined by annual precipitation patterns, range depletion, and recurring droughts (Jackson 1962). In years of average rainfall, food supplies and cover are abundant and probably not limiting to quail. During drought years, food resources are limited and competition highest. A drought year, or a series of 2 or more such years, will transform the available habitat from adequate to a shortgrass mesquite-parkland (Jackson 1947). Scaled quail seem to prefer more open habitats and may be better adapted to exploiting the habitats created during drought years. This ability, plus apparently differential effects on the 2 species as a result of predation (Jackson 1947), endoparasite loads (Rollins 1980), and effects of drought on reproduction, would seem to favor scaled quail in sympatric ranges.

Scaled quail increased their range dramatically in southwest Oklahoma during the early 1960's (Jacobs 1960) and have increased in Harmon County from Schemnitz's (1959) estimate of less than 100 birds. Data for bobwhite numbers for this area are unavailable, but Brown (1978) reported bobwhite populations have declined throughout the southwestern United States. Detailed, long-term population data for both species in sympatric ranges are necessary before conclusions can be made regarding the significance of competition in the ecology of these 2 game species.

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CHAPTER II

A COMPARISON OF CECAL NEMATODES FROM SYMPATRIC AND ALLOPATRIC BOBWHITE AND SCALED QUAIL[1]

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Abstract: Incidence and intensity of cecal nematodes collected from sympatric populations of bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) were compared with allopatric populations of bobwhite and scaled quail. Two species of cecal nematodes, *Aulonocephalus lindquisti* and *Subulura brumpti* were recovered. Sympatric bobwhites harbored a significantly ($P<0.01$) higher mean helminth burden than any of the other populations. An exchange of helminths apparently occurs between sympatric bobwhite and scaled quail. Scaled quail represent a new host record for *S. brumpti*.

INTRODUCTION

Numerous studies have been conducted on the helminth fauna of the bobwhite in the eastern portion of its range[3,7,11,14,18] and, to a lesser

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extent, on the western periphery[12,13,15,19] (Fig. 1). Conversely, a dearth of parasitological information exists for the scaled quail. Chandler[6] described a cecal nematode, Aulonocephalus lindquisti, which has been the only species of intestinal helminth reported in scaled quail.

While I was studying the ecology of sympatric bobwhite and scaled quail in mesquite (Prosopis glandulosa) grassland habitats[16], an opportunity arose to supplement the knowledge of helminth parasites of these 2 gamebirds. This study was initiated to determine the incidence, prevalence, and similarity of cecal nematodes of bobwhite and scaled quail in both sympatric and allopatric ranges.

MATERIALS AND METHODS

Quail were collected from 4 locations: three in Oklahoma including a sympatric site in Harmon County, and allopatric sites in Tillman and Comanche counties; and an allopatric scaled quail site in Eddy County, New Mexico. Mesquite was the principal woody plant on all 3 sites, with grass cover and height increasing along a west to east gradient. Mean annual rainfall varied from 33 cm in Eddy County, to 56 cm in Harmon County, to 74 cm in Comanche County. Other characteristics of the study areas were provided by Campbell et al.[5], Buck[4], and Barber[2].

Collections were made from November 1978 - February 1979 and November 1979 - January 1980 for the sympatric site. All allopatric bobwhites and scaled quail were obtained in late November. Quail were collected by shooting, utilizing hunter donations whenever available. Carcasses were placed in individual plastic bags, frozen, and dissected at a later date. The cecae were opened, the contents transferred to a

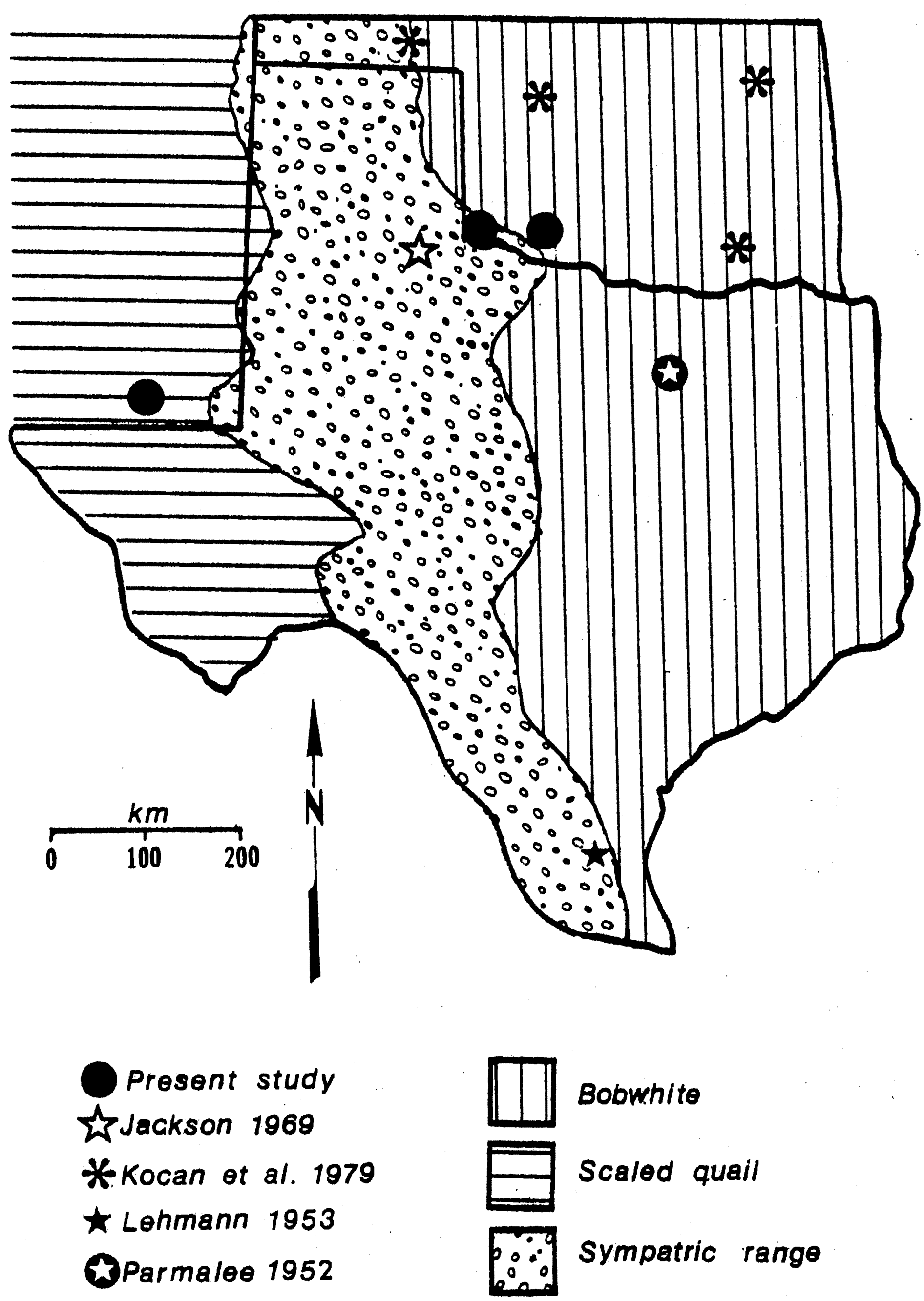

Figure 1. Distribution of bobwhite and scaled quail (Johnsgard 1975) and location of study sites. Symbols indicate sites of previous parasite studies on bobwhite in this region.

Petri dish, diluted with water, and examined grossly for helminths. The mucosa was then scraped and a second examination conducted. Nematodes were stored in 70% ethanol and cleared with lacto-phenol to facilitate identifications. Identifications were confirmed by Dr. A. C. Fusco, Animal Parasitology Institute, Beltsville, Maryland. Helminth burdens between populations were compared using Student's *t*-tests at the 0.05 level of significance.

RESULTS

Necropsies of 151 quail yielded 2 species of cecal nematodes, *Aulonocephalus lindquisti* and *Subulura brumpti*. Prevalence and intensity of cecal worms varied between sympatric and allopatric populations (Table 1). Time limitations and the large number of worms prohibited the identification of each individual worm. *A. lindquisti* and *S. brumpti* were very similar morphologically, and even with microscopic examination, differentiation between species was difficult. *A. lindquisti* was recovered from sympatric bobwhites and scaled quail, and from allopatric scaled quail, but was not found in allopatric bobwhites. *S. brumpti* was recovered from all populations. Mixed infections were found in the sympatric populations, but the total percentage of quail suffering simultaneous infections of *A. lindquisti* and *S. brumpti* was not determined.

Sympatric bobwhites harbored a significantly ($P<0.001$) higher mean worm burden than the other populations. Five of 39 (12.8%) sympatric bobwhites harbored more than 200 worms per bird. No significant differences in worm burden were observed between sympatric and allopatric scaled quail, or between allopatric bobwhite and scaled quail.

Table 1. Prevalence and worm burdens of cecal nematodes from bobwhite and scaled quail collected from 3 locations.

Population	Age Sex	N	% Infected	Mean worm burden[a]	Range
Allopatric bobwhites	Adult				
	Males	1	100	20.0	-
	Females	2	0	0.0	-
	Subtotal	3	33	6.7	0-20
	Immatures				
	Males	6	33	7.5	0-14
	Females	9	22	1.0	0-1
	Subtotal	15	27	4.2	0-14
	TOTAL	18	28	7.4	0-20
Allopatric scaled	Adult				
	Males	3	100	6.3	1-9
	Females	5	100	3.6	1-5
	Subtotal	8	100	4.6	1-9
	Immatures				
	Males	13	92	20.0	0-63
	Females	17	100	22.9	1-55
	Subtotal	30	97	21.7	0-63
	TOTAL	38	97	18.0	0-63
Sympatric bobwhites	Adult				
	Males	2	100	126.0	117-135
	Females	5	100	136.0	58-281
	Subtotal	7	100	133.0	58-281
	Immatures				
	Males	22	100	68.8	3-423
	Females	10	100	108.2	1-382
	Subtotal	32	100	81.1	1-423
	TOTAL	39	100	90.4	1-423

Table 1. (Continued).

Population	Age Sex	N	% Infected	Mean worm burden	Range
Sympatric scaled	Adult				
	Male	15	67	20.2	0-62
	Females	8	88	25.0	0-71
	Subtotal	23	74	22.2	0-71
	Immatures				
	Males	13	85	22.2	0-55
	Females	21	95	23.0	0-53
	Subtotal	34	91	22.7	0-55
	TOTAL	57	84	22.5	0-71

[a]Mean number of nematodes per infected quail.

The majority of the nematodes were found in the terminal pouches of the cecae, although occasionally they were recovered from the large or small intestine, presumably as a result of postmortem migration. Evidence of gross pathological change in the cecae was slight, even when heavy (>100 worms per bird) infections were found. The terminal portions of the cecae were inflamed in 3 of 56 (5.4%) sympatric scaled quail, possibly as a result of nematodes.

Mean worm burden per infected bird was higher in adult ($\bar{X}$=133.3, N=7) sympatric bobwhites as compared to immatures ($\bar{X}$=81.5, N=32), but the difference was not significant (P<0.12). In allopatric scaled quail, immatures (X=20.7, N=32) harbored a significantly (P<0.05) higher infection than adults ($\bar{X}$=4.6, N=6). Variations between age classes were not significant in sympatric scaled quail or allopatric bobwhites. Mean worm burdens for females ($\bar{X}$=105.5, N=17) were higher than for males ($\bar{X}$=75.8, N=22) in the sympatric bobwhite population, but the difference was not significant. There was likewise no significant difference in mean worm burdens between sexes in the other populations.

In sympatric bobwhites, mean worm burden more than doubled as the winter progressed (Table 2). Mean worm burden of sympatric scaled quail increased from November - January, but not as dramatically. Seasonal variation was not determined for allopatric populations due to collection schedules.

DISCUSSION

Results indicate that bobwhites sympatric with scaled quail harbor a higher endoparasite load than allopatric bobwhites. Jackson[9] found S. brumpti in 49 of 61 (81%) of the bobwhites analyzed, with a mean

Table 2. Winter occurrence and prevalence of cecal nematodes collected from sympatric bobwhite and scaled quail in Harmon County, Oklahoma during 1979-80.

Species	November		December		January	
	N	$\overline{X}$[a]	N	$\overline{X}$	N	$\overline{X}$
Bobwhite	8	51.0	20	84.7	11	123.2
Scaled quail	14	15.4	8	21.9	23	23.5

[a]Mean number of helminths per infected quail.

burden of 60. *A. lindquisti* was not reported by Jackson, although his study area was only 70 km southwest of my sympatric site. *A. lindquisti* was found in 97% of the bobwhites examined (*N*=627) in south Texas, but burdens were not high ($\bar{X}$=34.6)[13]. Parmalee[15] found a relatively low worm burden ($\bar{X}$=18.6) of *S. brumpti* in 6 bobwhites from an allopatric area in north-central Texas. Kocan et al.[12] surveyed bobwhites from 4 sites in Oklahoma, all allopatric, and found a low frequency of occurrence (27%, *N*=106) and a low worm burden ($\bar{X}$=19.8) of *S. brumpti*.

Parmalee[15], Jackson[9], and Kocan et al.[12] did not consider cecal worms to be detrimental to quail. However, the highest worm burden in any of these studies was reported by Jackson[9] ($\bar{X}$=60). The effects of much higher worm burdens, such as those found in sympatric bobwhites in the present study, are not known. My data suggest that worm burdens may approach 150 worms per bird, especially in the late winter months. Lehmann[13] found the highest worm burdens in late winter ($\bar{X}$=141, *N*=9), the period of highest mortality for quail, suggesting that high burdens of cecal nematodes may be of more concern than has been previously thought. Lehmann found that highest worm burdens coincided with lowest vitamin A levels in livers, both of which occurred in early March. The higher worm burdens during late-winter found in the present study are in accordance with Lehmann[13], but do not agree with data from Kocan et al.[12], who found that birds collected in summer had higher worm burdens than those collected in other seasons.

A. lindquisti has been reported from bobwhites[13,19], but only from areas where bobwhites are sympatric with scaled quail (Fig. 1). This suggests that *A. lindquisti* may be endemic to scaled quail. *S. brumpti* has been reported in bobwhites from Texas[9,15], Oklahoma[12], Ohio[17], and

Mississippi[18]. It seems plausible that an exchange of parasites may be occurring where bobwhite and scaled quail are sympatric. The life cycle of S. brumpti is indirect, involving arthropods as intermediate hosts[8]. The life cycle of A. lindquisti is unknown, but is probably similar to S. brumpti. A similarity of parasites in sympatric ranges should be related to the overlap of food habits of bobwhite and scaled quail. Arthropods are common items in the diets of bobwhites and scaled quail throughout the summer and fall. There was a high degree of overlap in fall-winter diets of bobwhite and scaled quail in Harmon County[16]. Mixed coveys of quail are not uncommon, and these may facilitate an exchange of parasites.

What differential effects, if any, S. brumpti and A. lindquisti have upon bobwhite and scaled quail is unknown. The effects of cecal parasites in bobwhites may be accentuated because of their much higher worm burdens. Barbehenn[1] proposed that certain parasites may be selected for in a host species because they are more detrimental to the host's competitors. In this manner, differential susceptibilities of bobwhite and scaled quail may allow for coexistence between them[1]. Additional parasitological studies of sympatric bobwhite and scaled quail from other areas of the sympatric range, incorporated with detailed population data for both species, is necessary to fully assess the possible correlation between parasites and their effects on sympatric species.

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CHAPTER III

ECOTYPIC CONVERGENCE IN SYMPATRIC BOBWHITE AND SCALED QUAIL[1]

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ABSTRACT. The effects of sympatric occurrence of bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) in southwest Oklahoma were investigated. Measurements of 14 morphological characters were compared between sympatric and allopatric sites. Attempts to evaluate the effects of competition, as revealed by character displacement, were confounded by ecotypic variation between study sites. Results indicated convergence has occurred in sympatric bobwhite and scaled quail for bill length from gape and gizzard mass, possibly as a result of similar diets. The potential for competitive displacement in sympatric ranges is discussed.

The sympatric occurrence of 2 or more closely related, ecologically similar species has prompted a plethora of research papers in the past. Many have concentrated on methods by which the potential competitors

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divide resources and thereby allow for coexistence in sympatric ranges (Vaurie 1951, Schoener 1965, Ficken et al. 1968, Cody 1974). One mechanism which promotes coexistence is character displacement (Brown and Wilson 1956) which appears to be a well accepted concept, even though some consider the evidence for character displacement weak (Grant 1972).

Bobwhite and scaled quail occur sympatrically over a large part of west Texas and portions of Oklahoma, Colorado, and New Mexico (Fig. 1). Both species inhabit shrub-forb grasslands and have similar diets (Schemnitz 1964, Rollins 1980) but different habitat preferences. Bobwhites prefer a more mesic habitat characterized by residual grass and brush cover (Hamilton 1962, Schemnitz 1964), whereas scaled quail prefer a more xeric habitat with more bare ground and less brush cover (Schemnitz 1964, Goodwin and Hungerford 1977).

The overlap in diets, and possibly nesting habitat (Reid et al. 1979), suggested that interspecific competition for resources was occurring. If interspecific competition has occurred, displacement patterns should have evolved to minimize competition and allow for coexistence (Cody 1974). According to Brown and Wilson (1956), morphological differences are accentuated in sympatric ranges resulting in a divergence of morphologies and less competition. Grant (1972) expanded this definition to include convergence, i.e. morphologies become more similar in sympatric ranges. The objective of this study was to determine if displacement patterns have occurred between allopatric and sympatric populations of bobwhite and scaled quail.

STUDY AREA AND METHODS. Quail were collected during fall-winter hunting seasons (20 November - 1 February) during 1978-79 and 1979-80. Bobwhites

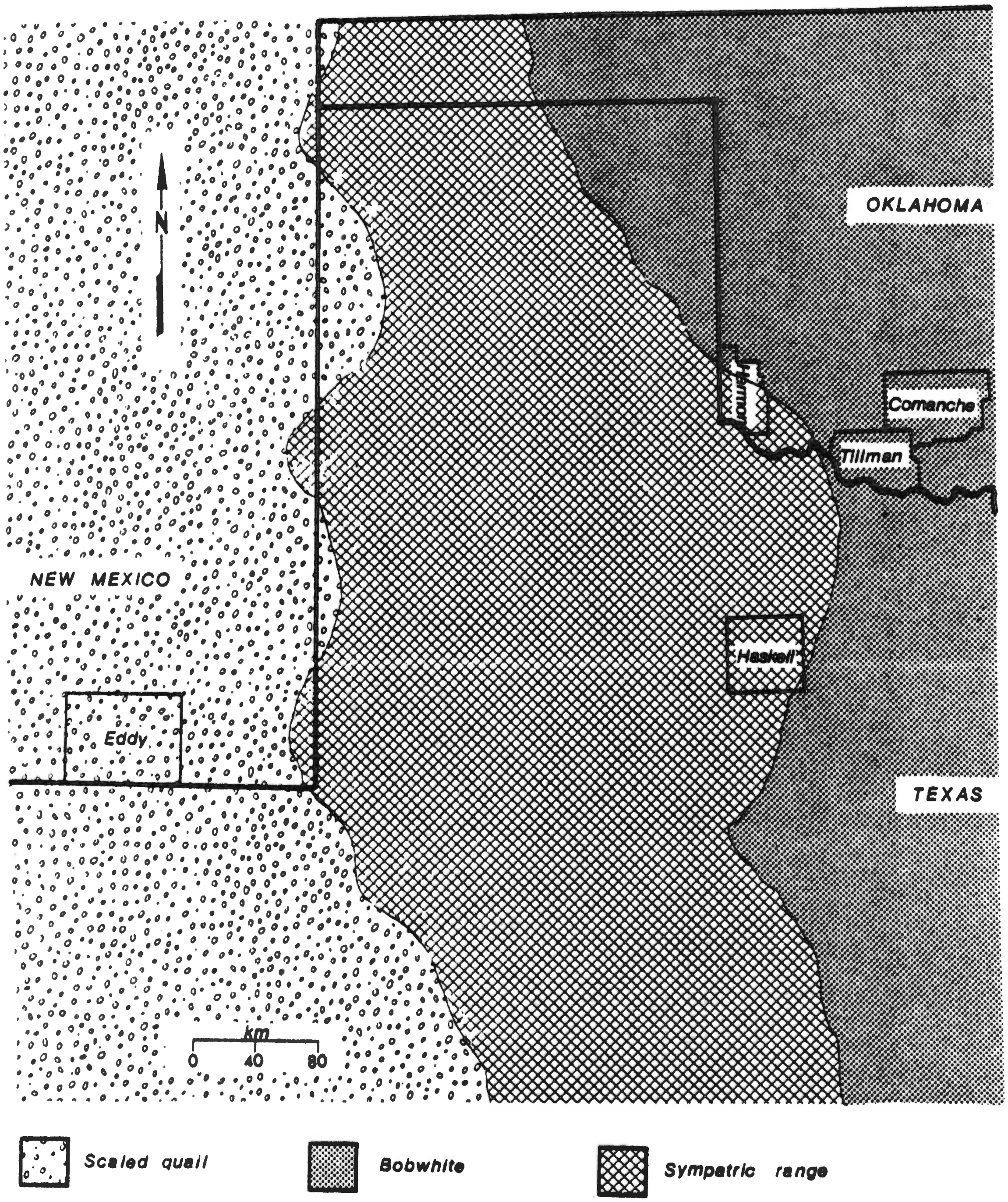

Figure 1. Distribution of bobwhite and scaled quail (Johnsgard 1975) in Oklahoma, Texas, and New Mexico, and location of study sites.

were collected from 2 sympatric (Harmon County, Oklahoma, and Haskell County, Texas) and 2 allopatric (Comanche and Tillman counties, Oklahoma) sites (Fig. 1). Scaled quail were collected from the Harmon County sympatric site and from an allopatric site (Eddy County, New Mexico). No scaled quail were collected from the Haskell County sympatric site. Relative densities of bobwhite:scaled quail at the sympatric sites were estimated at 50:50 at the Harmon County site, but approximately 80:20 at the Haskell County site. The majority of the sympatric bobwhites were collected from Harmon County. Sympatric bobwhite and scaled quail were collected within 1 km of one another. Sympatric quail in Harmon County would be considered syntopic (Rivas 1964). Bobwhites from these areas are *Colinus virginianus taylori*, while the scaled quail included both *Callipepla squamata pallida* (allopatric) and *C. s. hargravei* (sympatric) (Rea 1973).

Mesquite (*Prosopis glandulosa*) was the dominant woody species on all study sites. The major grasses were black grama (*Bouteloua eriopoda*) in Eddy County, blue and sideoats grama (*B. gracilis* and *B. courtipendula*) and buffalograss (*Buchloe dactyloides*) at the sympatric sites, and blue grama and little bluestem (*Schizachyrium scoparium*) at the allopatric bobwhite sites. Grass density and ground cover increased along a west-east annual precipitation gradient. Annual precipitation was 33 cm in Eddy County, 56 cm in Harmon County, and 77 cm in Comanche County. Other aspects of the study areas were described by Castetter (1956), Buck (1964), and Barber (1979).

Measurements were made of 13 external morphological characters: exposed culmen, bill length from gape, bill height and width, mandible width, head length and width, wing chord, forearm length, tarsus length,

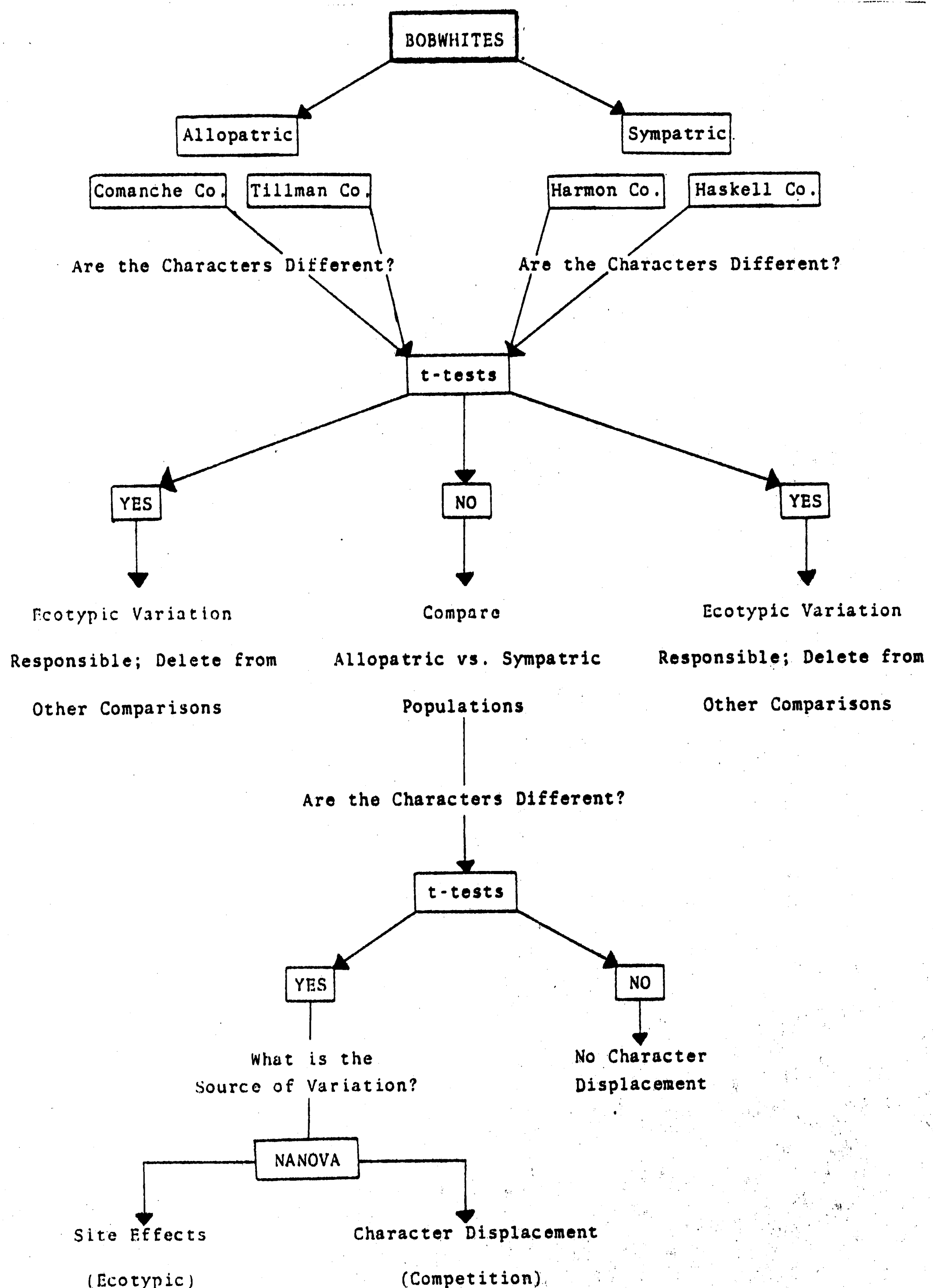

Figure 2. Flow chart of data analysis for adult bobwhites collected from populations sympatric and allopatric with scaled quail.

middle toe, middle claw, and hind toe with claw lengths. All external measurements were conducted according to Baldwin et al. (1931) and recorded to the nearest 0.1 mm. In addition to the external characters, gizzard mass was determined. The gizzard was halved and the contents removed, then measured to the nearest 0.1 cm^3 using water displacement.

The data were examined for differences within populations (due to age and sex differences), within sympatric and within allopatric populations of bobwhites (indicative of ecotypic variation), and between sympatric and allopatric populations (indicative of character displacement) (Fig. 2). Differences in morphological characters between different populations were analyzed using Student't *t*-test. In an attempt to separate effects due to competition from effects due to variation between study sites (i.e. ecotypic variation), a nested analysis of variance (NANOVA) (Sokal and Rohlf 1969) was conducted for all variables. Analyses were conducted using the Statistical Analysis System (Barr et al. 1979). The 0.05 level of significance was used in all comparisons.

RESULTS. Results of morphological measurements are presented in Tables 1 and 2 and Figure 3. Due to morphological differences between age classes, only adult birds were used for the comparisons. The use of immature birds would have afforded a larger sample size, but morphological differences as a result of different hatching dates (15 May - 1 October) preempted their use in comparisons. Appendix 1 presents the measurements of all birds segregated into age and sex classes.

Variation within sympatric and allopatric bobwhite sites. Allopatric bobwhites from Tillman County differed significantly from Comanche County bobwhites in bill length from gape ($P < 0.08$), bill width ($P < 0.03$), head

Table 1. Measurements (mm) of selected characters of sympatric and allopatric populations of adult bobwhite quail collected during fall-winter 1978-79 and 1979-80 from 4 sites in Oklahoma and Texas.

	Allopatric sites				Sympatric sites			
	Tillman Co.		Comanche Co.		Harmon Co.		Haskell Co.	
Character	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$
Culmen	4	14.6 ± 0.63	11	14.3 ± 0.46	11	14.1 ± 0.78	3	13.7 ± 0.58
Bill length from gape	4	17.5 ± 0.41	11	16.2 ± 1.29	11	16.0 ± 1.07	3	16.0 ± 0.00
Bill height	4	8.9 ± 0.48	10	9.1 ± 0.46	11	9.0 ± 0.52	3	8.7 ± 0.29
Bill width	4	9.6 ± 0.25	10	10.1 ± 0.46	11	10.0 ± 0.72	3	8.3 ± 0.29
Mandible width	4	8.0 ± 0.41	11	8.2 ± 0.61	11	8.7 ± 1.44	1	7.5
Head length	4	28.6 ± 0.48	10	27.1 ± 0.81	9	27.7 ± 0.79	3	28.5 ± 1.32
Head width	4	21.1 ± 0.48	10	20.5 ± 0.78	8	20.9 ± 0.44	3	20.7 ± 0.58
Wing chord	5	110.1 ± 2.41	12	107.2 ± 2.96	11	112.3 ± 3.50	0	
Forearm length	5	33.3 ± 0.95	12	33.1 ± 1.58	12	34.5 ± 2.88	0	
Tarsus	4	33.4 ± 0.95	12	32.7 ± 1.15	12	32.8 ± 1.36	3	33.0 ± 1.50
Middle toe	5	25.9 ± 1.24	12	26.3 ± 1.05	12	26.7 ± 1.51	3	26.0 ± 1.00
Middle claw	5	8.4 ± 1.29	12	8.5 ± 0.50	12	8.5 ± 0.54	3	9.2 ± 0.53

Table 1. (Continued).

	Allopatric sites				Sympatric sites			
	Tillman Co.		Comanche Co.		Harmon Co.		Haskell Co.	
Character	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$
Hind toe with claw	5	11.6 ± 0.42	12	12.3 ± 0.81	12	11.0 ± 0.66	3	11.3 ± 0.58
Gizzard mass[a]	2	5.8 ± 0.71	4	5.4 ± 0.29	12	4.4 ± 0.80	4	4.2 ± 0.57

[a] In cm^3.

Table 2. Measurements (mm) of selected characters of sympatric and allopatric populations of adult scaled quail collected from southwest Oklahoma and southeast New Mexico.

Character	Sympatric N	Sympatric $\bar{X} \pm$ SD	Allopatric N	Allopatric $\bar{X} \pm$ SD
Exposed culmen	23	13.4 ± 0.63	9	13.6 ± 0.42
Bill length from gape	23	15.9 ± 0.75	9	16.4 ± 0.82
Bill height	23	8.2 ± 0.58	9	8.2 ± 0.61
Bill width*	23	9.2 ± 0.52	9	8.8 ± 0.35
Mandible*	22	7.7 ± 0.67	9	7.3 ± 0.44
Head length	23	29.6 ± 1.23	9	29.6 ± 1.10
Head width	24	21.0 ± 0.90	9	20.5 ± 0.90
Wing chord	20	119.4 ± 3.89	1	122.0
Forearm length	19	37.2 ± 1.58	0	
Tarsus	24	34.0 ± 1.14	9	34.2 ± 1.18
Middle toe	25	25.2 ± 0.99	9	25.9 ± 1.39
Middle claw	25	9.2 ± 0.61	9	9.4 ± 0.70
Hind toe with claw*	25	10.4 ± 0.68	9	11.1 ± 0.78
Gizzard mass[a]**	39	4.9 ± 0.76	10	3.9 ± 0.56

[a] In cm^3

*$P < 0.05$

** $P < 0.01$

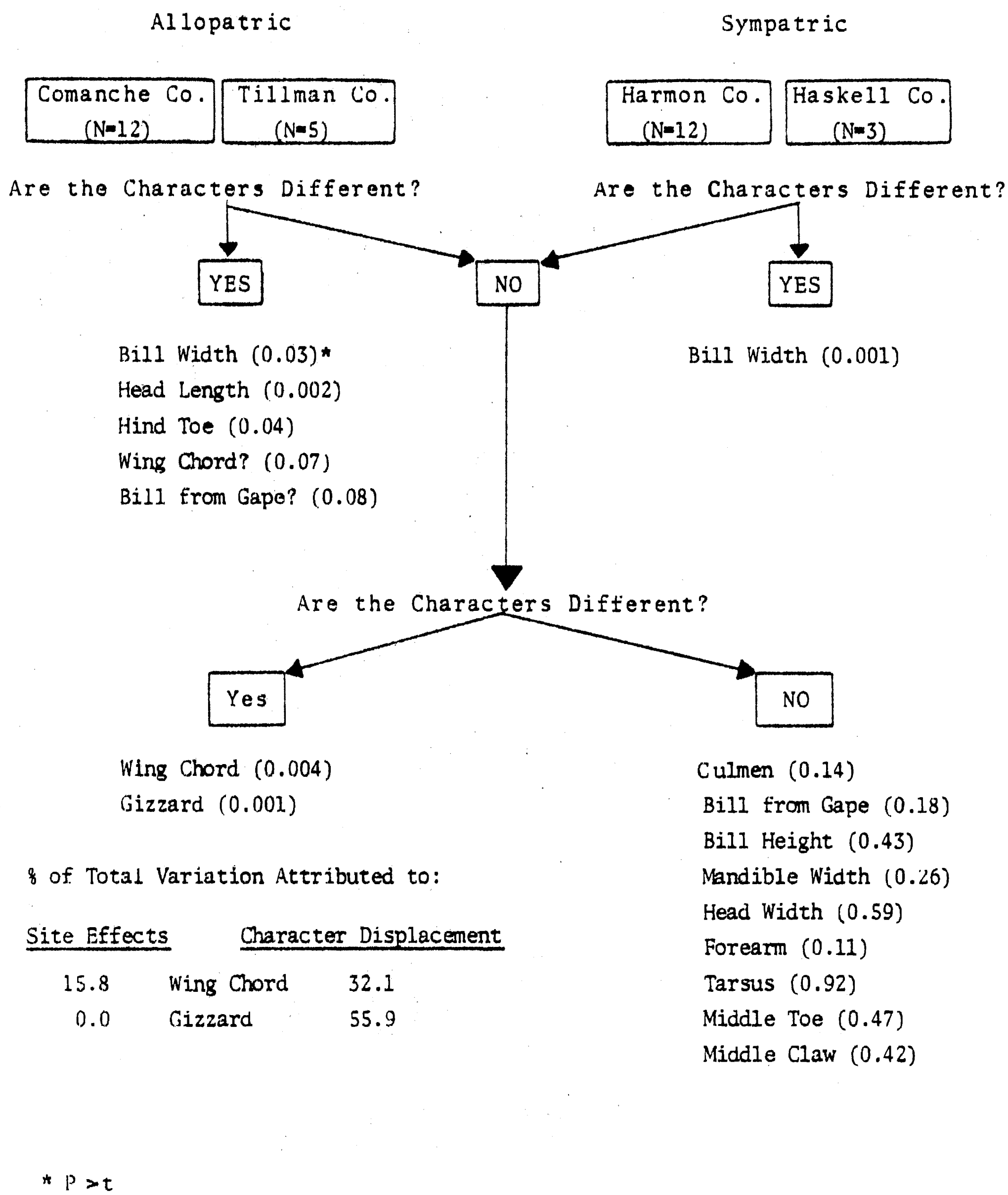

Figure 3. Flow chart of results from analysis of adult bobwhites collected from 4 sites in Oklahoma and Texas.

length ($\underline{P}<0.01$), hind toe with claw length ($\underline{P}<0.05$), and probably wing chord ($\underline{P}<0.07$). Sympatric bobwhites from Harmon County differed significantly from Haskell County bobwhites only in bill width ($\underline{P}<0.01$). Again, sample sizes were prohibitively small for Tillman ($\underline{N}=5$) and Haskell ($\underline{N}=3$) counties.

NANOVAs suggested that, for all characters except bill width and head length, variation between sympatric or between allopatric populations due to site effects was negligible (Table 3). The percentage of the total variation attributed to site effects exceeded or approached the error component only for bill width (65.7% of the total) and head length (49.4% of the total). Variation due to site differences varied from 0-17% for the remainder of the characters.

Variation between sympatric and allopatric populations. Sympatric and allopatric bobwhites were significantly different in wing chord ($\underline{P}<0.01$), hind toe with claw length ($\underline{P}<0.001$), and gizzard mass ($\underline{P}<0.05$). A NANOVA revealed that sympatry accounted for 32.1% of the total variation in wing chord, 42.4% of the total for hind toe with claw, and 55.9% of the total for gizzard mass. Variation due to sympatry ranged from 0-19% for the remaining characters.

Sympatric and allopatric scaled quail differed significantly in bill width ($\underline{P}<0.05$), mandible width ($\underline{P}<0.05$), hind toe with claw length ($\underline{P}<0.05$), and gizzard mass ($\underline{P}<0.01$). Because only 1 sympatric and 1 allopatric site were sampled, no measure of ecotypic variation was available, therefore, it was not possible to separate variation due to sympatry from that due to ecotypic differences. A NANOVA showed that site effects (sympatry plus ecotypic) accounted for 36.2% of the total variation for head length, 45.4% of the total for hind toe with claw,

Table 3. Breakdown of total variation into site, sympatry, and error components as determined by a NANOVA for 14 morphological characters of adult bobwhite quail.

	Percent of Total Variation Attributed to		
Character	Site	Sympatry	Error
Culmen	0.0	8.9	91.1
Bill length from gape	16.8	0.0	83.2
Bill height	0.0	0.4	99.6
Bill width	65.7	0.0	34.3
Mandible width	0.0	7.2	92.8
Head length	49.4	0.0	50.6
Head width	9.8	0.0	90.2
Wing chord	15.8	32.1	52.1
Forearm length	0.0	19.1	80.9
Tarsus	0.0	0.0	100.0
Middle toe	0.0	2.0	98.0
Middle claw	0.0	0.3	99.7
Hind toe with claw	8.2	42.4	49.4
Gizzard mass	0.0	55.9	44.1

and 40.0% of the total for gizzard mass. Variation due to site effects ranged from 0-27% of the total for the other characters.

Variation between sympatric bobwhite and scaled quail. Sympatric bobwhite and scaled quail differed significantly ($P \le 0.05$) for all characters except bill length from gape, head width, and gizzard mass. Allopatric bobwhite and scaled quail were different for all characters except bill length from gape, head width, and middle toe length.

DISCUSSION. Morphological variation existed between sympatric and allopatric populations of bobwhite and likewise for scaled quail. However, variation in itself does not preclude character displacement. Patterns which resulted from interspecific competition are confounded by both geographic (clinal, ecotypic) (James 1970, Power 1969, Fretwell 1969) and seasonal (Fretwell 1972) variation. The seasonal aspect of variation in the present study may have been minimized, as all samples were collected within a 3 month period (November - January). Ecotypic variation was evidenced by significant differences between bobwhites from the 2 allopatric sites (Comanche versus Tillman counties) and also by differences between sympatric sites (Harmon versus Haskell counties). Indeed, the inability to distinguish displacement as a result of competition from displacement as a result of other environmental factors has been a major weakness of character displacement studies to date (Grant 1972, Soule 1972).

Brown and Wilson's (1956) definition of character displacement does not include a convergence in sympatry, as does Grant's (1972) definition. Using Brown and Wilson's definition, only one character, middle toe length, exhibited character displacement. Middle toe length was not significantly different ($\underline{P}$<0.50) between allopatric bobwhite and scaled quail, but was significantly different ($\underline{P}$<0.01) in sympatry. In bobwhites, middle toe length increased from allopatry to sympatry, while in scaled quail, middle toe length decreased from allopatry to sympatry. The selection pressure operating on middle toe length is unknown, but might be related to habitat preferences (i.e. percentage of bare ground) of bobwhite and scaled quail.

Any attempt to explain the observed patterns of variation would be highly speculative. However, some correlations seem to be present between the observed patterns and these quails' ecologies.

Cody (1974) suggested that bill size may be less susceptible to displacement as a result of factors other than competition, and therefore changes in bill size better reflect the occurrence of interspecific competition for food. Sympatric bobwhite and scaled quail exhibited an apparent convergence for bill length from gape and gizzard mass. Similarities in food habits of 2 species in structurally simple habitats (such as quail habitat in Harmon County) tend to promote convergence in bill structures (Cody 1974). Rollins (1980) and Schemnitz (1964) found that fall-winter diets of sympatric bobwhite and scaled quail were very similar. Gizzard mass is correlated with food items (Marshall 1961) and would therefore also tend toward convergence.

Ecotypic variation in wing chord may have occurred along an east to west gradient for both species. James (1970) found wing lengths increased along east-west gradients for 12 species of birds measured. He suggested the increase in wing length was related to warmer temperatures and functioned in heat loss. I believe the longer wing lengths in the western sites may be related to a behavioral trait. Upon being flushed, quail tend to fly to the nearest, most dense cover. As density of brush cover decreased from east to west, a flight resulting from a flush would presumably be longer in the more western habitats. Increased wing lengths, and subsequent increased wing surface area, would seem to facilitate the longer flights, and thus be adaptive.

Some characters seemed to be more plastic to selection pressure than others. Bill width was significantly different ($P \leq 0.05$) between each of the 4 bobwhite sites and each of the 2 scaled quail sites. Hind toe with claw lengths were significantly different between sympatric and allopatric sites for both bobwhite and scaled quail. Other characters, i.e. exposed culmen, head width, and tarsus, were relatively unchanged between populations.

Adaptations to a changing habitat. Mesquite is renowned for its range expansions in Texas (Fisher 1978) and Oklahoma (Greer 1964). Mesquite is an effective competitor with grasses for soil moisture, therefore as mesquite density increases, less grass is produced, and grazing of rangeland is intensified. Overgrazing by livestock is one of the major factors affecting quail habitat in the Southwest (Brown 1978). As livestock deplete the available grass cover, the habitat becomes more open; an unfavorable situation for bobwhites. Scaled quail, however, prefer this more open type habitat and are therefore presumed to be better adapted at exploiting the resultant habitats.

I propose that, as mesquite increases, accompanied by livestock overgrazing, selection is occurring which favors quail better adapted to more open habitats. This would help to explain the apparent convergence of some characters for sympatric bobwhite and scaled quail in Harmon County. Convergence in sympatry is a consequence of each species responding similarly to its physical environment (Grant 1972, Wiens 1977). Convergence in morphologies should proceed until the species become similar enough to intensify interspecific competition. After this level has been attained, a divergence should be selected for to minimize interspecific competition and allow coexistence. If interspecific competition is occurring, it should force each species to retreat to its most optimal habitat where that species is best adapted to meet the competition from each other (Svardson 1949).

If competition has occurred between bobwhite and scaled quail, the scaled quail may be the better competitor because of its habitat preferences. Should this be the case, a decrease in the range of bobwhites should be anticipated. Indeed, Brown (1978) stated that bobwhites, along with other grassland gamebirds with the exception of the scaled quail, had experienced a marked reduction in range throughout the Southwest. Conversely, scaled quail have increased their ranges westward (Brown 1973) and eastward (Jacobs 1960), and have increased dramatically in density in Harmon County since Schemnitz's (1959) estimate of fewer than 100 birds.

If the environmental conditions are changing so that each species is favored alternately, coexistence would be possible even if competition was occurring (Crombie 1947, Hutchinson 1948, Wiens 1977). Quail production in the sympatric area is controlled ultimately by seasonal rainfall (Jackson 1962). Jackson (1962) described the series of events leading to population oscillations in bobwhites in the Rolling Plains as:

> (1) a drought of several years, coupled with livestock overgrazing, depleted the majority of bobwhites due to a lack of suitable habitat; (2) a year of increased rainfall allowed secondary succession of a wide variety of forbs, the seeds of which were staples in the bobwhite's diet; (3) a year of above normal rainfall

> followed, covering the range with dense stands of broomweed (Gutierrezia) which provided excellent cover for bobwhites and allowed them to increase dramatically and occupy even the marginal habitats; (4) plant succession favored the replacement of forbs by grasses, which decreased the seed production of the habitat and subsequently bobwhite populations; (5) several drought years occurred which continued the pattern.

Scaled quail production does not seem to suffer from drought conditions as does bobwhite production (Schemnitz 1964). This ability coupled with the mesquite-parkland (Jackson 1947) habitat created during drought years should favor scaled quail. As the drought is broken by several years of above normal rainfall, the habitat seems to be better suited for bobwhites, which would increase while scaled quail might decrease. The eastward edge of the sympatric zone moves from east to west with major rainfall trends (A. S. Jackson, pers. comm.).

In summary, bobwhite and scaled quail exhibited a convergence in morphologies, possibly in response to habitat changes brought about by recurring droughts and the increase of mesquite. Additional research, especially long term population data from sympatric ranges, is needed to assess fully the role of interspecific competition in the ecology of sympatric bobwhite and scaled quail.

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APPENDIX

MEASUREMENTS (mm) OF BOBWHITE AND SCALED QUAIL COLLECTED FROM SYMPATRIC AND ALLOPATRIC POPULATIONS

Table 1. Measurements (mm) of bobwhite and scaled quail collected from sympatric and allopatric populations.

Species / Character / Population	All samples N	All samples $\bar{X} \pm SD$	Adult males N	Adult males $\bar{X} \pm SD$	Adult females N	Adult females $\bar{X} \pm SD$	Imm. males N	Imm. males $\bar{X} \pm SD$	Imm. females N	Imm. females $\bar{X} \pm SD$
BOBWHITE										
Exposed Culmen										
Allopatric										
Comanche Co.	41	14.3 ± .49	4	14.1 ± .25	7	14.4 ± .53	15	14.3 ± .59	14	14.2 ± .43
Tillman Co.	14	14.2 ± .66	3	14.7 ± .76	1	14.5	4	13.6 ± .48	5	14.3 ± .57
Sympatric										
Harmon Co.	62	13.9 ± .59	5	14.5 ± .71	6	13.8 ± .75	32	13.8 ± .52	19	13.9 ± .58
Haskell Co.	20	13.5 ± .49	2	13.5 ± .71	1	14.0	7	13.4 ± .45	10	13.5 ± .53
Bill from gape										
Allopatric										
Comanche Co.	41	16.5 ± .93	4	15.8 ± 1.71	7	16.5 ± 1.04	14	16.1 ± .79	15	17.0 ± .45
Tillman Co.	14	17.5 ± .66	3	17.3 ± .29	1	18.0	5	17.1 ± 1.03	5	17.8 ± .42
Sympatric										
Harmon Co.	60	16.1 ± 1.18	5	16.5 ± .95	6	15.6 ± 1.07	30	16.0 ± 1.26	19	16.2 ± 1.16
Haskell Co.	20	16.2 ± .91	2	16.0 ± 0.0	1	16.0	7	16.1 ± .99	10	16.3 ± 1.03
Bill height										
Comanche Co.	38	9.0 ± .45	4	9.1 ± .48	6	9.1 ± .49	15	9.1 ± .46	13	8.8 ± .43
Tillman Co.	14	8.8 ± .38	3	9.0 ± .50	1	8.5	4	8.6 ± .25	5	8.7 ± .45
Sympatric										
Harmon Co.	63	8.7 ± .52	5	8.7 ± .57	6	9.2 ± 1.07	33	8.8 ± .42	19	8.7 ± .67
Haskell Co.	19	8.3 ± .56	2	8.7 ± .35	1	8.5	7	8.3 ± .57	9	8.2 ± .62

Table 1. (Continued).

Species Character Population	All samples N	All samples $\bar{X} \pm$ SD	Adult males N	Adult males $\bar{X} \pm$ SD	Adult females N	Adult females $\bar{X} \pm$ SD	Imm. males N	Imm. males $\bar{X} \pm$ SD	Imm. females N	Imm. females $\bar{X} \pm$ SD
Bill width										
Allopatric										
Comanche Co.	39	10.1 ± .47	4	10.1 ± .25	6	10.1 ± .59	15	10.1 ± .50	14	10.1 ± .49
Tillman Co.	14	9.6 ± .29	3	9.7 ± .29	1	9.5	4	9.5 ± 0.0	5	9.7 ± .45
Sympatric										
Harmon Co.	62	9.8 ± .74	5	9.5 ± .61	6	10.3 ± .61	32	9.8 ± .73	19	9.8 ± .79
Haskell Co.	19	8.8 ± .47	2	8.5 ± 0.0	1	8.0	7	9.0 ± .29	9	8.9 ± .55
Mandible width										
Allopatric										
Comanche Co.	40	8.3 ± .60	4	8.1 ± .48	7	8.3 ± .70	14	8.3 ± .47	15	8.3 ± .73
Tillman Co.	13	8.0 ± .38	3	8.0 ± .50	1	8.0	4	7.9 ± .25	4	8.0 ± .58
Sympatric										
Harmon Co.	57	8.3 ± 1.04	5	8.5 ± .87	6	8.9 ± 1.86	28	8.1 ± .98	18	8.3 ± .86
Haskell Co.	18	7.5 ± .36	1	7.5	0		7	7.5 ± .41	10	7.4 ± .37
Head length										
Allopatric										
Comanche Co.	38	27.1 ± 1.00	5	27.0 ± .91	6	27.2 ± .82	14	27.5 ± 1.24	14	26.7 ± .73
Tillman Co.	15	28.3 ± .70	3	28.8 ± .29	1	28.0	4	28.4 ± .75	6	27.8 ± .68
Sympatric										
Harmon Co.	61	28.2 ± .91	2	27.8 ± 1.04	6	27.6 ± .74	32	28.5 ± .98	20	27.9 ± .60
Haskell Co.	21	28.3 ± .91	2	29.2 ± .35	1	27.0	8	28.4 ± 1.15	10	28.2 ± .63

Table 1. (Continued).

Species / Character / Population	All samples N	All samples $\bar{X} \pm SD$	Adult males N	Adult males $\bar{X} \pm SD$	Adult females N	Adult females $\bar{X} \pm SD$	Imm. males N	Imm. males $\bar{X} \pm SD$	Imm. females N	Imm. females $\bar{X} \pm SD$
Head width										
Allopatric										
Comanche Co.	37	20.3 ± .91	4	20.1 ± .48	6	20.8 ± .88	13	20.7 ± .75	14	19.9 ± .95
Tillman Co.	15	20.7 ± .67	3	21.3 ± .29	1	20.5	4	20.1 ± .96	6	20.5 ± .55
Sympatric										
Harmon Co.	60	20.5 ± .92	3	2.12 ± .29	5	20.7 ± .45	32	20.4 ± 1.05	20	20.4 ± .83
Haskell Co.	21	20.1 ± .65	2	21.0 ± 0.0	1	20.0	8	20.4 ± .64	10	19.8 ± .54
Wing chord										
Allopatric										
Comanche Co.	42	108.3 ± 3.01	4	108.5 ± 3.0	8	106.5 ±2.88	14	110.5 ± 1.86	16	107.2 ± 2.90
Tillman Co.	16	108.8 ± 2.24	4	110.2 ± 2.8	1	109.5	4	109.3 ± 1.89	6	107.5 ± 2.07
Sympatric										
Harmon Co.	60	111.7 ± 3.44	4	113.0 ± 3.6	7	111.9 ± 3.63	31	111.5 ± 3.53	18	111.7 ± 3.42
Haskell Co.	0		0		0		0		0	
Forearm length										
Allopatric										
Comanche Co.	42	33.5 ± 1.22	3	33.7 ± 1.5	8	32.9 ± 1.66	14	33.9 ± 1.11	17	33.5 ± .99
Tillman Co.	13	33.5 ± 1.09	4	33.2 ± .87	1	33.5	4	34.0 ± 1.47	3	32.8 ± 1.15
Sympatric										
Harmon Co.	56	34.2 ± 1.89	4	35.0 ± 2.8	7	34.3 ± 3.09	27	33.9 ± 1.60	18	34.6 ± 1.54
Haskell Co.	0		0		0		0		0	

Table 1. (Continued).

Species / Character / Population	All samples N	All samples $\bar{X} \pm SD$	Adult males N	Adult males $\bar{X} \pm SD$	Adult females N	Adult females $\bar{X} \pm SD$	Imm. males N	Imm. males $\bar{X} \pm SD$	Imm. females N	Imm. females $\bar{X} \pm SD$
Tarsus										
Allopatric										
Comanche Co.	44	32.8 ± 1.23	4	32.6 ± 1.49	8	32.7 ± 1.07	15	33.3 ± 1.18	17	32.3 ± 1.16
Tillman Co.	16	32.8 ± .98	4	33.4 ± .95	0		5	32.5 ± .94	6	32.6 ± .97
Sympatric										
Harmon Co.	67	33.1 ± 1.26	5	33.4 ± 1.52	7	32.3 ± 1.52	34	33.0 ± 1.07	21	33.3 ± 1.49
Haskell Co.	23	32.5 ± .86	2	33.8 ± 1.06	1	31.5	9	32.2 ± .79	11	32.5 ± .74
Middle toe										
Allopatric										
Comanche Co.	44	26.5 ± 1.18	4	26.8 ± 1.23	8	26.1 ± .95	15	27.0 ± .99	17	26.1 ± 1.32
Tillman Co.	17	26.0 ± 1.28	4	26.0 ± 1.06	1	25.5	5	25.6 ± 1.71	6	26.4 ± 1.11
Sympatric										
Harmon Co.	65	26.7 ± 1.42	5	26.7 ± .76	7	26.6 ± 1.95	33	26.8 ± 1.58	20	26.7 ± 1.14
Haskell Co.	21	26.2 ± .83	2	26.5 ± .71	1	25.0	8	25.8 ± .96	10	26.6 ± .47
Middle Claw										
Allopatric										
Comanche Co.	42	8.7 ± .57	4	8.5 ± .71	8	8.4 ± .82	14	8.9 ± .86	16	8.8 ± .68
Tillman Co.	17	8.3 ± .78	4	8.6 ± .38	1	7.5	5	8.1 ± .22	6	8.3 ± .68
Sympatric										
Harmon Co.	66	8.6 ± .72	5	8.8 ± .47	7	8.4 ± .56	34	8.7 ± .71	20	8.5 ± .83
Haskell Co.	23	8.7 ± .82	2	10.0 ± .71	1	7.5	9	8.7 ± .75	11	8.6 ± .71

Table 1. (Continued).

Species / Character / Population	All samples N	All samples X̄ ± SD	Adult males N	Adult males X̄ ± SD	Adult females N	Adult females X̄ ± SD	Imm. males N	Imm. males X̄ ± SD	Imm. females N	Imm. females X̄ ± SD
Hind toe with claw										
Allopatric										
Comanche Co.	44	12.5 ± .78	4	12.4 ± .75	8	12.2 ± .89	15	12.7 ± .77	17	12.5 ± .77
Tillman Co.	17	11.7 ± .64	4	11.5 ± .41	1	12.0	5	11.6 ± .55	6	11.9 ± .86
Sympatric										
Harmon Co.	66	11.3 ± .81	5	11.3 ± .55	7	10.9 ± .75	34	11.4 ± .87	20	11.3 ± .78
Haskell Co.	24	11.0 ± .64	2	10.0 ± .71	1	11.0	9	10.9 ± .65	12	10.9 ± .67
Gizzard mass[a]										
Allopatric										
Comanche Co.	23	5.1 ± .73	2	5.5 ± .28	2	5.2 ± .28	8	4.6 ± .51	11	5.4 ± .81
Tillman Co.	8	5.6 ± .43	1	5.3	1	6.3	1	5.8	5	5.5 ± .41
Sympatric										
Harmon Co.	51	4.7 ± .71	7	4.5 ± .28	5	4.3 ± .84	24	4.6 ± .59	14	5.0 ± .72
Haskell Co.	23	3.9 ± .67	0		3	4.1 ± .61	12	3.8 ± .56	7	4.1 ± .89
SCALED QUAIL										
Exposed Culmen										
Allopatric	41	13.4 ± .59	3	13.8 ± .45	6	13.5 ± .45	12	13.4 ± .53	20	13.2 ± .68
Sympatric	75	13.1 ± .60	16	13.6 ± .65	7	13.0 ± .29	19	13.0 ± .46	33	12.9 ± .55
Bill length from gape										
Allopatric	41	16.4 ± 1.11	3	15.5 ± .50	6	15.3 ± .98	12	16.5 ± 1.29	20	16.5 ± 1.16
Sympatric	75	16.1 ± .94	16	16.0 ± .72	7	15.6 ± .79	19	16.3 ± .98	33	16.2 ± 1.02

Table 1. (Continued).

Species Character Population	All samples N	All samples $\bar{X} \pm SD$	Adult males N	Adult males $\bar{X} \pm SD$	Adult females N	Adult females $\bar{X} \pm SD$	Imm. males N	Imm. males $\bar{X} \pm SD$	Imm. females N	Imm. females $\bar{X} \pm SD$
Bill height										
Allopatric	41	8.0 ± .49	3	8.7 ± .58	6	7.9 ± .49	12	8.2 ± .49	20	7.9 ± .34
Sympatric	76	8.0 ± .44	16	8.3 ± .58	7	8.0 ± .58	20	8.0 ± .32	33	8.0 ± .38
Bill width										
Allopatric	41	9.0 ± .68	3	9.0 ± 0.0	6	8.8 ± .42	12	8.8 ± .42	20	9.1 ± .75
Sympatric	75	8.9 ± .64	16	9.2 ± .36	7	9.1 ± .80	20	8.9 ± .57	33	8.6 ± .67
Mandible length										
Allopatric	33	7.3 ± .58	3	7.8 ± .29	6	7.0 ± 0.0	9	7.3 ± .35	15	7.4 ± .77
Sympatric	73	7.2 ± .64	15	7.7 ± .65	7	7.7 ± .66	19	7.2 ± .50	32	6.9 ± .50
Head length										
Allopatric	39	29.3 ± 1.20	3	29.3 ± .58	6	29.7 ± 1.33	12	29.9 ± 1.26	18	28.8 ± 1.02
Sympatric	74	29.5 ± 1.09	15	30.1 ± 1.0	8	28.6 ± .94	20	30.0 ± 1.01	31	29.2 ± .92
Head width										
Allopatric	39	20.6 ± .68	3	20.8 ± .66	6	20.3 ± .98	12	20.9 ± .56	18	20.5 ± .61
Sympatric	76	21.0 ± .93	16	21.2 ± .80	8	20.6 ± 1.03	20	21.1 ± .60	32	20.8 ± 1.10
Wing chord										
Allopatric	21	118.1 ± 2.86	0		1	122.0	7	118.9 ± 2.28	12	117.0 ± 2.78
Sympatric	64	117.3 ± 3.02	12	120.5 ± 3.2	8	117.6 ± 2.61	14	118.2 ± 2.61	30	115.4 ± 3.25

Table 1. (Continued).

Species Character Population	All samples N	All samples X̄ ± SD	Adult males N	Adult males X̄ ± SD	Adult females N	Adult females X̄ ± SD	Imm. males N	Imm. males X̄ ± SD	Imm. females N	Imm. females X̄ ± SD
Forearm length										
Allopatric	19	35.8 ± 1.65	0		0		7	35.9 ± 1.84	11	35.8 ± 2.00
Sympatric	61	36.3 ± 1.65	12	37.6 ± 1.5	8	36.6 ± 1.50	14	36.2 ± 1.12	28	35.7 ± 1.71
Tarsus										
Allopatric	42	33.6 ± 1.20	3	34.8 ± 1.1	6	33.9 ± 1.02	13	33.7 ± 1.03	19	33.2 ± 1.25
Sympatric	78	33.7 ± 1.08	15	34.1 ± 1.4	9	33.9 ± 1.33	20	34.2 ± .80	34	33.3 ± 1.03
Middle toe										
Allopatric	43	25.7 ± 1.31	3	26.2 ± .29	6	25.8 ± 1.72	12	26.5 ± .71	21	25.1 ± 1.34
Sympatric	76	25.3 ± 1.22	16	25.1 ± .96	9	25.4 ± 1.07	19	25.8 ± 1.18	32	25.1 ± 1.35
Middle claw										
Allopatric	44	10.8 ± .92	3	11.7 ± .58	6	10.8 ± .75	13	10.7 ± .93	21	10.7 ± .98
Sympatric	79	10.5 ± .74	16	10.3 ± .63	9	10.7 ± .75	20	10.4 ± .61	34	10.2 ± .86
Gizzard mass[a]										
Allopatric	44	4.4 ± .82	4	3.9 ± .51	6	3.9 ± .64	12	4.6 ± .84	22	4.4 ± .85
Sympatric	100	5.0 ± .75	23	4.9 ± .78	16	4.8 ± .74	23	5.1 ± .79	38	5.1 ± .73

[a] In cm^3

VITA

Dale Rollins

Candidate for the Degree of

Master of Science

Thesis: COMPARATIVE ECOLOGY OF BOBWHITE AND SCALED QUAIL IN MESQUITE GRASSLAND HABITATS

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